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Supplemental Information

Unique Cellular Organization in the Oldest Root Meristem

Alexander J. Hetherington, Joseph G. Dubrovsky, and Liam Dolan

Supplemental Information

Geological locality of *R. carbonica* and *Apex 76.1*

Apex 76.1 was identified on thin section 76 of the Oxford University Herbaria's slide collection. The thin section was made by James Lomax petrologist [S1], from a coal ball collected from Dulesgate – one of the key localities of the Lancashire and Yorkshire coal field dated to Westphalian A (Bashkirian) (319–317 million years old) [S2–S5]. Thin section 81 on which *R. carbonica* was discovered is believed to come from a similar collection locality as *Apex 76.1*. In the collections of the Oxford University Herbaria there are no thin sections which correspond or form a series with either thin section 76 or 81.

Assigning *Apex 76.1* to the species *Lyginopteris oldhamia*

The cellular structure of the root cap, apical and sub-apical root portions are well preserved in *Apex 76.1* (Figure 1A). The cellular organisation of *Apex 76.1* indicates that it was not actively growing when preserved; cell expansion has proceeded to the extreme apex (Figure 2B). The maximum diameter of the root in the section is 313 µm. The section is oblique, but closer to the median plane in the distal region (nearest the root tip). The provascular cylinder (Figure 1A' green) is narrow, 86 µm in diameter, and consists of seven cell layers. The ground tissues are split into two distinct tissue types, the endodermis (Figure 1A' brown) and cortex (Figure 1A' orange). Outside the ground tissues is a single epidermis layer (Figure 1A' blue). The root cap (Figure 1A' yellow) is inconspicuous and is four layers thick at the most distal root cap region. Cell walls in the central most region of the root cap are not aligned in register typical of the columella of extant roots [S6]. The largest cells in the cap are the distal-most cells in the central cap region, and peripheral cells in the lateral-root-cap proximal portion, indicating a pattern of gradual maturation and sloughing typical of roots of extant species. All cell file converge on a group of cells that constitute the remains of the differentiated promeristem (Figure 1A' pink). Based on its size and tissue organisation we tentatively assign *Apex 76.1* to *Lyginopteris oldhamia* based on similarities with the previously published description of *Lyginodendron oldhamium* [S7,S8] (Figure 1B, B') later designated *Lyginopteris oldhamia* (see [S9,S10]) which was collected at the same geological locality as *Apex 76.1*.

The diameter of *Apex 76.1* is larger (313 µm) than the *Lyginopteris oldhamia* apex described by Stopes and Watson [S7] which is 280 µm at its widest point (Figure 1B, B'). The ground tissue comprises two distinct tissues in *Apex 76.1 and L. oldhami*a a single cell layer of endodermis (Figure 1A', B' brown) and a multiple cell layered cortex (Figure 1A', B' orange).There is a single layer of epidermis in both root apices (Figure 1A', B' blue). The main difference between the two apices is that the *L. oldhamia* root cap (Figure 1A', B' yellow) (Figure 1B') is larger than *Apex 76.1* (Figure 1A'). The length of the *L. oldhamia* root cap (Figure 1B') is 460 µm from the most distal to the most proximal point, compared to 285 µm on *Apex 76.1* (Figure 1A'). (Figure 1B'), The distance from the most distal region of the differentiated *L. oldhamia* promeristem to the most distal portion of the cap is 124 µm long and contains approximately 8 cells along the root axis. In contrast the corresponding region on *Apex 76.1* (Figure 1A') is roughly half the size (60 µm long and with approximately 4 cells). The overall similarity in the tissue organisation, root size and differentiated promeristem structure allowed us to tentatively assign *Apex 76.1* to *Lyginopteris oldhamia*.

Radix carbonica systematic Palaeobotany

Subdivision: Tracheophyta

Class, Order and Family: Incertae sedis

Genus: *Radix* Hetherington, Dubrovsky et Dolan gen. nov.

Species*: Radix carbonica* Hetherington, Dubrovsky et Dolan sp. nov.

Combined diagnosis: A large, blunt shaped root meristem in which the Körper complex constitutes the stele and almost all the ground tissue whereas the Kappe complex comprises the root cap and the cell file abutting the root cap interpreted as the epidermis. The root cap is distinct from the other tissues of the meristem. Cells of the root cap are typically larger and darker – due to the accumulation of opaque material within and between cells – than cells in the proximal region of the root. Most of the promeristem cells are arranged in a broad columella-shaped

structure abutting the procambium, ground tissues proximally and root cap distally. The distal region of the promeristem is characterised by the presence of many anticlinal cell divisions.

Etymology: Generic name *Radix* is the Latin noun for root. Specific name *carbonica* is the Latin adjective for coal, because this fossil was found in a coal ball.

Type: *Radix carbonica sp. nov.*

Holotype: Thin section 81 Oxford University Herbaria (Figure 1C)

Repository: Oxford University Herbaria (Oxford, United Kingdom).

Type locality and age: Thin section 81 lacks a collection locality but the coal ball from which the thin section was prepared is believed to have been collected from the Lancashire and Yorkshire coal field, dated to Westphalian A (319–317 million years old) [S2–S5] (Bashkirian) in age along with the comparable thin sections housed in the Oxford University Herbaria.

Description: The cellular organisation of *R. carbonica* is well preserved; cell outlines are clearly demarcated. The presence of a root cap (Figures 1C, 3A, B yellow) covering the apex indicates that this is a root apex. The number of cell layers in the root cap decreases proximally. Consequently the root cap tapers rapidly and is almost completely lost in the proximal region of the preserved apex indicating a pattern of gradual maturation and sloughing typical of roots of extant species. The root apex is 1.65 mm in length (from the distal-most point of the root cap to where it leaves the plain of section in the proximal-most region of the root). The apex is 1.55 mm in diameter at its widest point 1.01 mm from the tip of the root cap. It tapers slightly, forming a blunt apex, 1.19mm in diameter at the level of the meristematic initials (Figure 3A pink). The apex is divided clearly into the three main tissue types characteristic of root meristems – the root cap (Figure 3A, B yellow), epidermis combined with ground tissues (Figure 3A, B orange) and procambium (Figure 3A, B green). The promeristem is located at the point of convergence of theses tissues [S11] (Figure 3A, pink) and is the group of cells from which all the fundamental tissues of the root develop [S11]. The exceptional preservation allows identification of these tissues and the initials from which they developed (Figure 3A, B pink and lilac).There are 138 initials when viewed in median longitudinal section in the *R. carbonica* promeristem comprising two morphologically distinct groups of initials. First, the proximal promeristem initials (Figure 3B pink) are rounded with an average circularity of 0.83 (where 1 – is a perfect circle) (standard error (SE) 0.01, $n = 31$ cells). Second, the distal promeristem initials (Figure 3B lilac), are more box shaped with an average circularity of 0.80 (SE 0.008, $n = 107$ cells) making these initials morphologically distinct from each other $P = 0.008$ (*t*-Test). Promeristem size and organisation – 138 cells in longitudinal section arranged in two morphologically distinct pools of initials – marks *R. carbonica* as distinct from all other previously described fossil apices.

Cellular organisation of *R. carbonica* is different from all other root apices for the Carboniferous Period

R. carbonica differs from all other fossil root apices [S7,S8,S12–S17] because it is the first and only example of a root apex fossilised during active growth. The cellular organisation in the actively growing *R. carbonica* apex differs from all other non-growing Carboniferous root apices in two further ways. First there are many more cells within the *R. carbonica* promeristem than in the differentiated promeristems of *Apex 76.1* (Figure 1A, A'), *L. oldhamia* (Figure 1B, B') [S7,S8,S13], *Amyelon* [S12,S14] and *Psaronius* [S16]. Second the *R. carbonica* apex is over three times larger in diameter than *Apex 76.1*(Figure 1A, A'), *L. oldhamia* (Figure 1A, B) [S7,S8,S13] and *Amyelon* [S12,S14]. Comparisons cannot be made with the root meristem described by Dennis [S15] because the promeristem structure in that specimen is obscured. The large diameter of the *R. carbonica* apex and with the large number of cells which constitute the promeristem demonstrate that *R. carbonica* is distinct from all other previously described fossil root apices.

Comparison of *R. carbonica* with the root meristems of vascular plants

Roots are classified into distinct classes [S6,S18–S25] on the basis of the organisation of cells within the meristem. The cellular organisation of *R. carbonica* was compared with all previously described meristem types to determine if it could be classified into any of the existing root meristem classes.

<u>*R. carbonica* is different from all extant lycophyte root meristems</u>

The lycophytes are the earliest diverging group of extant vascular plants [S26]. Lycophytes comprises three clades [S26–S28] – the Selaginellales, Lycopodiales and Isoetales – each with a distinct root meristem organisation. There is a single tetrahedral apical cell in the majority of *Selaginella* species which have been described (Figure 4E) [S29–S36] although some species have more than one initial [S36,S37]. *R. carbonica* with its multicellular pomeristem consisting of 138 cells is distinct from all *Selaginella* species with a single tetrahedral apical cell. Additionally *R. carbonica* is distinct from *Selaginella* species with multicellular pomeristems [S36,S37]. In *Selaginella* species with multiple initials the initials are arranged in three tiers [S36,S37], whereas the initials of *R. carbonica* are organised in over 10 tiers a number far greater than any *Selaginella* species described to date.

Multicellular promeristems consisting of either three [S36,S38–S40] or four [S36,S40–S43] tiers of initials develop in Lycopodiales root apices (the most ancient extant clade of the lycophytes [S26,S27]) (Figure 4E). Schüepp [S21] classified the Lycopodiales root meristems into his IIID group. The procambium and ground tissue comprise the Körper complex, and the root cap comprises the Kappe complex. The epidermis develops independently of the Körper and Kappe; and is located between the two complexes. The cellular organisation of *R. carbonica* is different from the Lycopodiales meristem organisation in at least two ways. The first and most striking difference between *R. carbonica* and extant Lycopodiales is the size and organisation of the promeristem. The promeristem of *R. carbonica* is broad and contains over 10 tiers of cells which far exceeds the 3 or 4 tiers described in extant Lycopodiales. Second, the epidermis of *R. carbonica* is not distinct from all other layers but instead is interpreted to develop as the innermost layer of the Kappe complex. There are similarities between *R. carbonica* and the root meristem of *Lycopodium clavatum* [S32] which develops a domain with initials that are not clearly separated into distinct tiers. However, unlike *L. clavatum* [S32] where there is a central group of many initials, the *R. carbonica* promeristem is organised in a regular block of cells in a columnar arrangement.

The promeristem of the Isoetales forms either two [S36,S44–S47] or three tiers [S36,S41,S48,S49] of initials (Figure 4E).The *R. carbonica* promeristem is much larger than Isoetales; there are over 10 tiers of cells in the *R. carbonica* promeristem and only three in typical Isoetales root meristems. In summary the size and organisation of the *R. carbonica* promeristem distinguishes it from all extant lycophytes.

The organisation of the *R. carbonica* promeristem is different from all extant monilophyte root meristems

The monilophytes are a single monophyletic group that includes the ferns and horsetails [S27,S50–S52]. There is a single apical initial in most monilophyte root meristems [S36,S53–S55] (Figure 4E). However there are more than one initials in the Marattidae and the Osmundaceae where they range between 1 and 4 [S36,S53,S54,S56–S59]. The broad multicellular promeristem of *R. carbonica* consisting of 138 cells is therefore strikingly larger than the promeristems of all extant monilophytes with either a single or a small number of initials cells. In summary the size and organisation of the *R. carbonica* promeristem distinguishes it from all extant monilophytes.

R. carbonica most closely resembles extant gymnosperm meristems

The root meristems of gymnosperms are distinctive from the meristems of other vascular plants because of the presence of a broad promeristem with common initials for all or the majority of the mature tissues of the root [S18–S21,S38]. In gymnosperms all mature tissues converge on a broad promeristem which takes the form of an upturned cup shape (the base of the cup is where the procambium and root cap columella converge and the sides of the cup are where the ground tissue, epidermis and lateral root cap converge (Figure 4)). The initial cells in the central region of the promeristem are arranged as a columella where the columnar organisation results from the alignment of longitudinal cell walls in files, which Allen [S60,S61] refers to as the ‘column mother initial zone’ [S60,S61]. Individual sets of initials for specific tissue types are not distinct. There are three types of initial cell organisation in gymnosperm promeristems. 1. There is a common set of initials for all fundamental tissues or all fundamental tissues except the vasculature tissues (Cycadales [S62–S67]; Ginkgoales [S62,S68–S70] and some members of the Pinopsida [S60,S61,S71,S72]. 2. There is one set of common initials for the root cap columella and the procambium and another set for all of the ground tissue, epidermis and lateral root cap [S63,S73–S76] which is referred to as the ‘conifer type’ [S63,S76] (Pinopsida and Cupressophyta). 3. There is one set of common initials for ground tissue, epidermis and lateral root cap and another set of initials for root cap columella and procambium (Gnetophyta) [S63,S70,S77,S78].

The organisation of cells in *R. carbonica* is more similar to the cellular organisation of meristems in extant gymnosperms than any other group of tracheophytes. The *R. carbonica* promeristem like the promeristems of all gymnosperms is broad and shaped like an upturned cup and cells in the central region are organised as a columella. *R. carbonica* most closely resembles the promeristem organisation characteristic of the Cycadales, Ginkgoales and some members of the Pinopsida because the promeristem of both comprises a set of common initials for all fundamental tissues except the vascular tissues. However, it is distinct from all of these extant gymnosperms in three main ways. First the position of the Körper-Kappe boundary. Second, the discrete nature of the *R. carbonica* root cap. Third, the presence of anticlinal cell divisions in a regular broad promeristem – as discussed in detail in the main text.

R. carbonica is not an angiosperm root meristem

R. carbonica cannot be an angiosperm root. First, it is approximately 320 million years old and angiosperms did not appear in the fossil record until almost 200 million years later [S79]. Second, the cellular organisation in the *R. carbonica* promeristem is entirely different from any of the recognised 15 classes of angiosperm meristem [S6].

In summary the root meristem of *R. carbonica* is most similar to extant gymnosperm meristems because all fundamental tissues converge on a broad promeristem with a regular columella-like organisation. However, the three major differences between *R. carbonica* and typical gymnosperm meristems are the position of the Körper-Kappe boundary, the discrete nature of the *R. carbonica* root cap and the presence of anticlinal cell divisions in a regular broad promeristem – as discussed in the main text. These three character states combined mark *R. carbonica* as distinct from all root meristems previously described.

Description of the Körper-Kappe theory

Schüepp [S21,S80] identified that root meristems could be split into two discrete zones defined by the distribution of two distinct cell division types termed Körper (inner body) and Kappe (outer cap) T-divisions. When a root meristem in viewed in median longitudinal section files of cells can be followed from the initials to the mature regions of the root. Occasionally a single cell file splits in two and this break leads to the formation of characteristic T shape (where the horizontal stroke of the T represents a transverse cell division and the vertical stroke of the T represents the longitudinal division and the split of one cell file into two). T-divisions can be found throughout the root meristem however the orientation of the T shape varies. Within the Körper (body) complex the vertical stroke of the vertically inverted T points away from the meristematic initials towards the base of the root – resulting from the transverse cell division occurring before the longitudinal division [S11,S21,S80–S82]. Inverted T-divisions where the vertical stroke of the T points away from the meristematic initials facilitate increase in cell layer number within the root body and therefore termed Körper T-divisions (Figure 4). However, within the Kappe (cap) the vertical stroke of the T points towards the meristematic initials resulting from the longitudinal division occurring before the transverse division [S11,S21,S80–S84]. T divisions where the vertical stroke of the T points away from the meristematic initials facilitate increase in cell number within the root cap and therefore termed Kappe T-divisions (Figure 4). The distribution of Körper and Kappe T-divisions therefore defines the Körper-Kappe boundary, and critically the position of this boundary varies between species and provides a way to distinguish between different classes of root meristems [S11,S21,S80–S82,S84].

Extended Figure 4 legend

Figure 4 displays a summary of meristem types in the extant vascular plant lineages. The Selaginellales are shown to have a single tetrahedral apical cell, as is found in the majority of *Selaginella* species (Figure 4E) [S29–S36]. The root apices of the Lycopodiales are shown with initials arranged in either three [S36,S38–S40] or four [S36,S40–S43] tiers, representing the promeristem structure in the majority of the Lycopodiales described to date. The promeristem of the Isoetales is depicted with initials arranged in either two [S36,S44–S47] or three tiers [S36,S41,S48,S49] as described in all Isoetales examined to date (Figure 4E).

The root meristems of monilophytes are depicted in Figure 4E with a single apical initial. We hypothesize that there was a single initial in the root meristem of the last common ancestor of the monilophytes (Fig, 4E). The most recent monilophyte phylogenies indicate that there is a single initial in the root meristem of the basal monilophytes taxa [S52]; Equisetales [S36,S53,S85,S86] and the Ophioglossales [S36,S54,S87–S89]. Osmundales and Marattiales develop between 1 and 4 initials and there are single initials in the six more derived

classes (Hymenophyllales, Gleicheniales, Schizaeles, Saliniales, Cyatheales and Polypodiales). Given that the most basal monilophyte lineages develop root meristems with single initials, and clades with a single apical (initial) cell are more common than those with multiple initials, it is most parsimonious to conclude that a single apical (initial) cell was the ancestral root meristem state in the monilophytes and that multiple initials subsequently evolved in the ancestors of the Osmundales and Marattiales. Therefore the root meristems of monilophytes are depicted with a single apical initial in Figure 4E.

The gymnosperm root meristem in Figure 4E comprises a central zone of common initials for all tissues, or common initials for all non-vascular tissues and a separate set for all vascular tissues. The meristem is shown with common initials for all tissues or common initials for all non-vascular tissues and a separate set for all vascular tissues because this is the most parsimonious interpretation for the ancestral root meristem type in gymnosperms. A root meristem with common initials for all tissues or all non-vascular tissues is found in the Cycadales [S62–S67]; Ginkgoales [S62,S68–S70] and some members of the Pinopsida [S60,S61,S71,S72] which are the most ancestral lineages of the gymnosperms [S27,S90–S93].

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